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FRESHWATER TRICLADS (TURBELLARIA) OF NORTH AMERICA. XVI. MORE ON SUBTERRANEAN SPECIES OF *PHAGOCATA* OF THE EASTERN UNITED STATES

Roman Kenk

Abstract.—Three new species of *Phagocata* are described, *P. pygmaea* and *P. spuria* from caves in North Carolina, and *P. notorchis* from a seep in eastern Tennessee. Additional distributional records are given for *P. carolinensis* and *P. procera.*

The species discussed in this paper were collected by several investigators, mainly speleologists, in the course of several years. In order to obtain an accurate picture of the shape of living planarians, which can hardly be maintained by any known method of preservation, I had asked my collaborators to send me live specimens. Another good reason to insist on living specimens is the fact that many flatworms are collected in the immature state, lacking their reproductive systems which form the basis of their taxonomic standing. They may be either juveniles that have not yet achieved sexual maturity, or specimens that have been subjected to prolonged starvation for the lack of proper food. It is known that planarians may sustain starvation for several months without detriment. They gradually reduce some parts of their anatomy, decrease in size, and cannot be distinguished from juveniles. It is highly probable that many of the immature planarians collected in the field, particularly those inhabiting subterranean waters, are not true juveniles but specimens that have been kept from full development or have reduced in size and structure on account of deficient nutritive conditions. These immature specimens may be raised to maturity in the laboratory by being kept in aquaria under proper temperature conditions and being fed once or twice a week. Species of *Phagocata* accept beef liver as food and mature after several months in the culture.

Methods

Mature specimens were preserved by killing well extended worms with a hot aqueous solution of mercuric chloride ($HgCl_2$), acidulated with acetic acid after the killing. Serial sections of 6–8 μm thickness were stained with Ehrlich's acid hematoxylin and counterstained with Eosin-Phloxine B.

The type specimens of the new species have been deposited in the National Museum of Natural History (formerly United States National Museum, USNM), Smithsonian Institution, Washington, D.C.

Phagocata notorchis, new species
Figs. 1A, B, 2, 3

Type material.—Holotype: posterior part of worm, sagittal sections on 4 slides (USNM 102760). Paratypes: sagittal sections of entire animal, 7 slides (USNM 102761); sagittal sections of posterior part, 4 slides (USNM 102762); transverse sections of posterior part, 7 slides (USNM 102763).

External features. (Fig. 1A, B).—This white, blind, very slender species reaches a considerable size, up to a length of 27 mm and a width of 2 mm when quietly gliding. The anterior end is truncate, with a slightly convex frontal margin and a pair of slender,

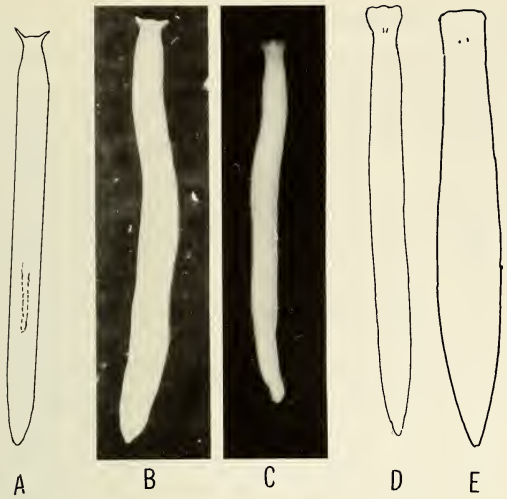

Fig. 1. Drawings and photographs of living specimens. A and B, *Phagocata notorchis*; C and D, *P. pygmaea*; E, *P. morgani*.

pointed auricles projecting anterolaterally and held elevated when in gliding motion. Behind the auricles the body margins widen, then run parallel for the greater part of the body length, to narrow again near the bluntly pointed posterior end. The pharynx is situated in the posterior third of the body. Thus the species externally resembles two other white *Phagocata* species of the Appalachian region that have prominent auricles, *P. bursaperforata* Darlington and *P. procera* Kenk, from which it is clearly separated by its anatomical characters.

Anatomy.—The branching of the intestine could not be analyzed in the living specimens. There are very many, certainly over 20, lateral branches on either side of the anterior intestinal trunk, and perhaps an equal number on each posterior trunk.

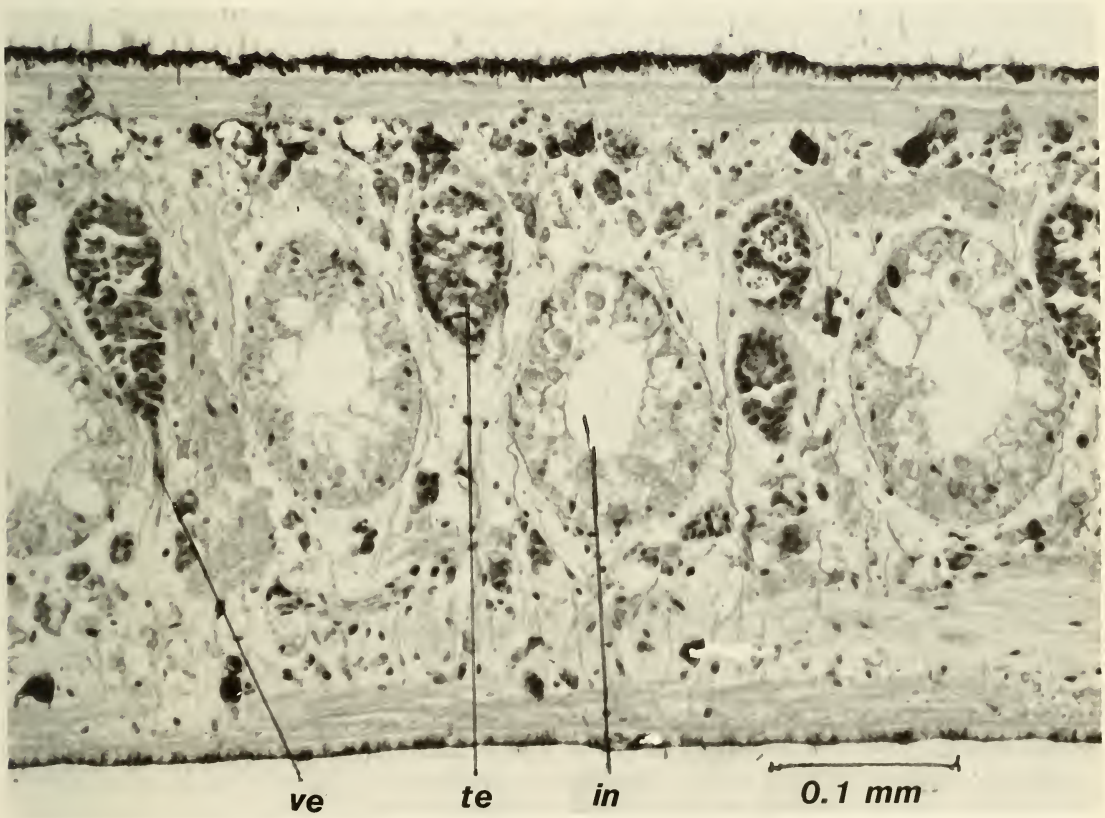

Fig. 2. *Phagocata notorchis,* sagittal section through anterior region. *in,* intestine; *te,* testis; *ve,* vas efferens.

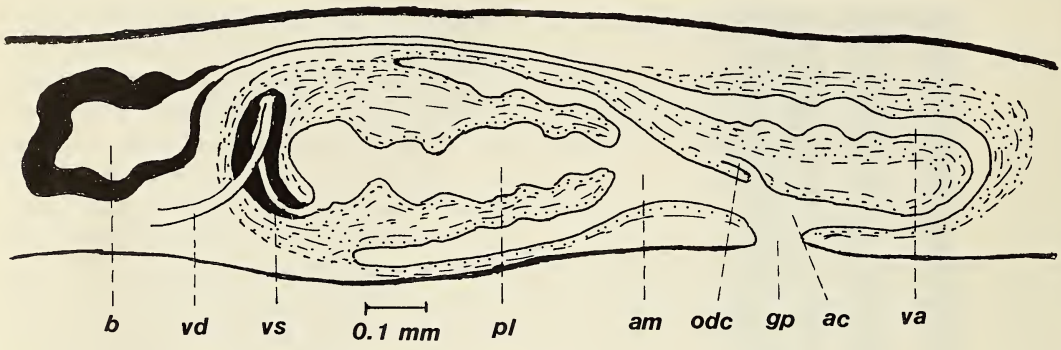

Fig. 3. *Phagocata notorchis*, semidiagrammatic view of copulatory apparatus in sagittal section. *ac*, common atrium; *am*, male atrium; *b*, copulatory bursa; *gp*, gonopore; *odc*, common oviduct; *pl*, penis lumen; *va*, vagina; *vd*, vas deferens; *vs*, seminal vesicle.

In the reproductive system, the ovaries are located behind the third to fifth pair of intestinal branches. The testes (Fig. 2) are predominantly subdorsal, situated above and between the intestinal branches. The follicles are not directly attached to the thin anterior vas deferens, as they are in many other species of the genus, but connect with it by individual efferent ductules (*ve*). The testicular zone on either side begins at a considerable distance posterior to the ovaries and extends to about the level of the pharynx root.

In the copulatory apparatus (Fig. 3), the gonopore leads into a small common atrium that connects anteriorly with the male atrium and posteriorly with the outlet of the copulatory bursa. The penis consists of a small bulb and a plug-shaped papilla. Its lumen is divided into an anterior seminal vesicle (*vs*) situated in the bulb and a large cavity (*pl*) that would correspond to an ejaculatory duct. The vesicle is lined by a thick epithelium of tall, apparently secretory, cells. In sagittal sections it appears as a dorsoventrally oriented duct, but extends also laterally in the bulb, so as to represent an anteroposteriorly compressed cavity. Ventrally it opens into the large cavity in the penis papilla, which is lined by a cuboidal epithelium and surrounded by a strong muscular layer. The walls of this cavity are variously folded and the cavity opens into the male atrium in a place dependent on the state of contraction of the muscular systems of the cavity and the external wall of the papilla. The two vasa deferentia, after expanding into the usual spermiductal vesicles, enter the penis bulb laterally and open separately into the dorsal portion of the seminal vesicle.

The two oviducts or ovovitelloducts unite in the space above the atrium and the short common oviduct (*odc*), equipped with eosinophilic shell glands, opens into the common atrium (*ac*) from the dorsal side. The copulatory bursa (*b*), a cavity with irregular outline, is located a short distance posterior to the pharyngeal pouch. Its outlet, the bursal duct, runs posteriorly somewhat to the left of the midline, and is divided into two different section. The anterior section is a narrow canal proceeding along the male atrium, surrounded by a moderate muscle layer. The posterior section or vagina (*va*), however, is greatly expanded and curves ventrally to open into the common atrium. It has a very thick muscular layer composed of intermingled fibers. There is no communication between the bursa and the intestine.

Distribution and ecology.—The species was collected by J. J. Lewis and T. Everitt on 7 May 1977 in Great Smoky Mountains National Park, in a seep near the trail to Alum Cave Bluffs, Sevier County, Tennes-

see, at an altitude of about 4900 feet (circa 1500 meters). About 20 specimens were sent to me alive, the majority of them immature. From its blindness and occurrence in a seep we may consider the species to be a groundwater inhabitant.

Taxonomic position.—The species belongs to a group of *Phagocata* widely distributed in the Appalachian region and apparently related to the subgenus *Atrioplanaria.* Its most outstanding characteristic is the presence of a large vagina with an extraordinarily developed muscle coat. A large vagina, but without excessive musculature, is seen also in *P. procera.* The dorsal position of the testes is also a good character, that is approached also in *P. bursaperforata.*

Etymology.—The species name, *notorchis* (Greek *noton,* dorsum; *orchis,* testis) refers to the subdorsal position of the testicular follicles.

Phagocata procera Kenk

Phagocata procera was described by Kenk (1984) from Cat Den Cave in Jackson County, North Carolina, but is more widely distributed in caves and springs in that state. The characteristic features of the species, apart from the presence of elongated pointed auricles and ventral prepharyngeal testicles, are in the differentiation of the copulatory apparatus. The penis lumen consists of two sections with histologically different linings, an anterior "seminal vesicle" with a tall, glandular epithelium and a posterior "ejaculatory duct" lined by a nonglandular cuboidal epithelium. Both sections may vary considerably in their appearance in preserved specimens, due to muscular contractions and distortions. The anterior section receives many faintly cyanophilic gland ducts and may appear as a cavity or a convoluted duct. The posterior section may have the aspect of a canal or of a wide cavity of irregular outline, opening on the dorsal side or at the tip of the penis papilla. The bursal duct widens gradually as it proceeds posteriorly and acquires a strong muscle coat to form a vagina, without altering the histological appearance of its epithelial lining.

Additional distributional records, all in North Carolina:

Burke County: Flatworm Fissure, located in Linville Gorge Wilderness Area, 13 May 1984, six immature specimens collected in two small pools by Cato O. Holler, Jr. and Christopher Holler and shipped to me alive; they matured in a laboratory culture.—Fifty/Fifty Fissure, in Linville Gorge Wilderness Area, near Linville Falls, 23 Sep 1984, 5 specimens collected by Cato O. Holler and his family and Lee James in a small seep; shipped to me alive.

McDowell County: Lake Tahoma Cave, located on the road up Little Buck Creek near Lake Tahoma, just outside of Marion, 4 Jan 1985, 4 specimens collected by Cato O. Holler, Jr. and Christopher Holler in a small seep and shipped alive.

Mitchell County: Buckshot Cave, 9 Sep 1979, in a seep in the cave 5 specimens collected by Cato O. Holler, Jr. and shipped to me alive.

Yancey County: Seep on State Road 128, 1.5 miles north of Blue Ridge Parkway, at about 6000 feet (circa 1830 m) altitude, 5 Jun 1972, 13 specimens collected by Leslie Hubricht and shipped preserved.—Seep on State Road 128, 10 Nov 1979, 3 specimens collected by Cato O. Holler, Jr. and Cathy Topping and sent alive.—Mt. Mitchell, Sep 1975, many specimens collected by Nicole Gourbault and Ian R. Ball and brought to me alive.

Phagocata pygmaea, new species
Figs. 1C, D, 4, 5

Type material.—Holotype: set of sagittal sections on 4 slides (USNM 102764). Paratype: sagittal sections on 3 slides (USNM 102765).

External features (Fig. 1C, D).—This is a small and slender white species, externally

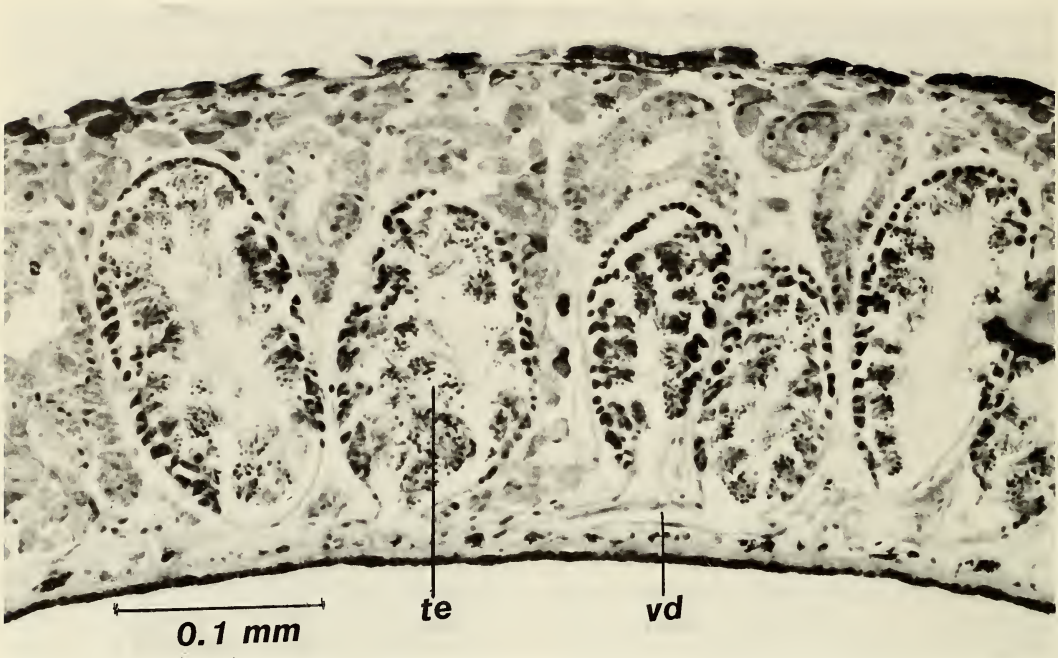

Fig. 4. *Phagocata pygmaea,* sagittal section through anterior region. *te,* testis; *vd,* vas deferens.

resembling several other species of the genus in the same general area. Mature specimens are about 10.5 mm long and 0.8 mm wide. The anterior end is truncate, with a slightly convex central part of the frontal margin and rounded lateral edges somewhat protruding laterally, lacking pointed auricles. There is an insignificant neck-like constriction, posterior to which the body widens again, the lateral margins remaining parallel for the greater part of the body length, to narrow again behind the level of the copulatory complex and to meet at the rather rounded posterior end. There are two small eyes (diameter of the pigment cups about 23 μm), situated very close together at a level rather far removed from the frontal margin of the head. The pharynx is inserted behind the middle of the body and measures about ⅛ the body length. The number of branches on the intestinal trunks could not be counted, but is certainly very large.

Anatomy.—The ovaries, equipped with parovaria, are situated behind the second or third lateral branches of the intestinal trunk. The numerous testes (Fig. 4) are prepharyngeal and are attached directly to the ventral sperm ducts or vasa deferentia. They must be considered to be essentially ventral, although many of the large follicles may extend between the intestinal branches far dorsally, occupying almost the entire dorsoventral diameter of the body.

In the copulatory apparatus (Fig. 5), that is located some distance behind the pharyngeal pouch, the gonopore leads into a small common atrium that connects anteriorly with the male atrium (*am*) and dorsally with the outlet of the bursal duct. The penis consists of a small, but highly muscular, bulb and a finger-shaped papilla. The penis lumen (*pl*) is a uniform, rather wide cavity, not divided into a seminal vesicle and an ejaculatory duct. It is confined mainly to the penis papilla and opens at the tip of the papilla. Its wall forms a number of villus-like projections. The vasa deferentia, that in their posterior parts form the enlarged and convoluted spermiductal vesicles filled with sperm, ascend dorsally at the level of the penis bulb, enter the bulb lat-

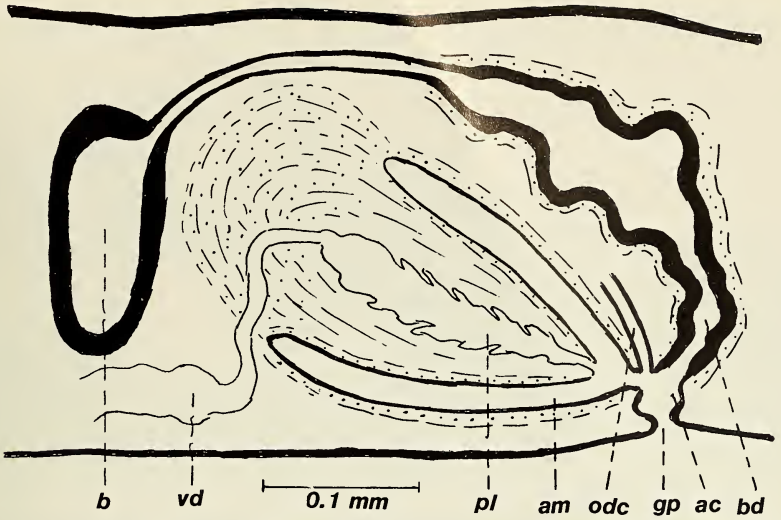

Fig. 5. *Phagocata pygmaea,* copulatory apparatus in sagittal section. *ac,* common atrium; *am,* male atrium; *b,* copulatory bursa; *bd,* bursal duct; *gp,* gonopore; *odc,* common oviduct; *pl,* penis lumen; *vd,* vas deferens.

erally, then curve posteriorly to open separately into the anterior end of the penis lumen. The two oviducts unite in the space between the male atrium and the bursal duct. The common oviduct thus formed opens from the dorsal side into the atrial cavity at the border between the male atrium (*am*) and the common atrium. The copulatory bursa is a rounded cavity without any special modifications. Its outlet, the bursal duct, is divided histologically into two sections. The anterior section is a straight narrow duct lined with a ciliated cuboidal epithelium. The posterior section is widened and somewhat convoluted and bends ventrally to reach the common atrium. Its lining epithelium consists of apparently secretory (apocrine) cells without cilia. Both sections are surrounded by moderate layers of muscular fibers.

Distribution and ecology. —*Phagocata pygmaea* was collected in Turtle Shell Cave, Stokes County, North Carolina, located at the base of Moore's Wall near Hanging Rock State Park, between Danbury and Moore's Springs. Seven immature specimens were taken by Cato O. Holler and Christopher Holler on 20 Nov 1983 and shipped to me alive. Some matured in the laboratory in a culture kept at 14°C and fed beef liver at weekly intervals.

Taxonomic position. —The species is closely related to the other subterranean species of *Phagocata* of the Appalachian area. Its outstanding characteristics are in the anatomy of the copulatory apparatus, mainly the structure of the penis and the differentiation of the bursal duct.

Etymology. —The name *pygmaea* (Latin, dwarfish) refers to the small size of the species.

Phagocata spuria, new species
Figs. 6, 7

Type material. —Holotype: set of sagittal sections on 4 slides (USNM 102766). Paratypes: sagittal sections of two specimens on 10 slides (USNM 102767, 102768).

External features. —This is a small, white, two-eyed species resembling the common sympatric *Phagocata morgani morgani* (Stevens and Boring) to such an extent that it was at first considered to be that species. No sketches or photos were prepared of living specimens (see Fig. 1E of *P. morgani*). The anterior end is truncate, with a more or less straight frontal margin and rounded

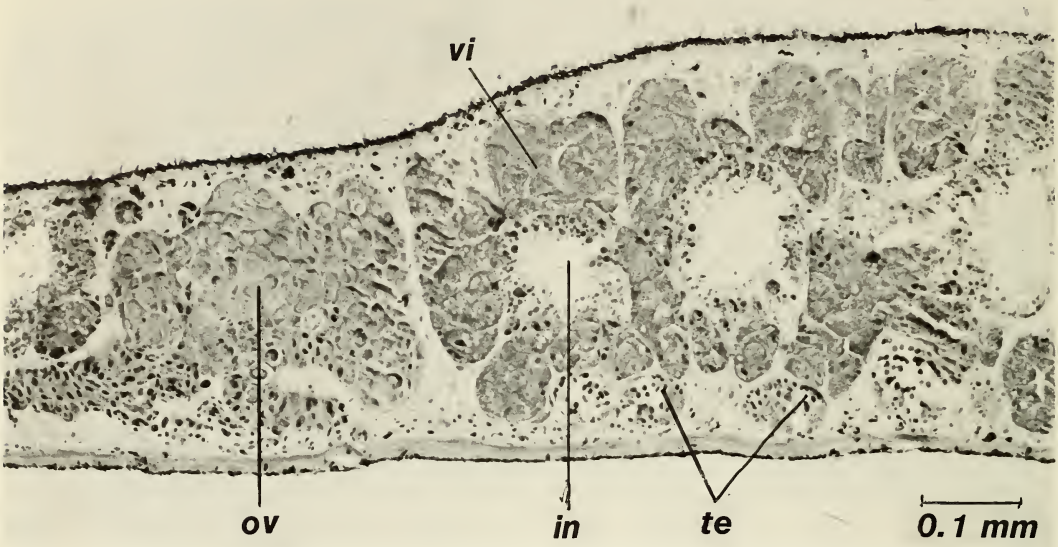

Fig. 6. *Phagocata spuria,* sagittal section through anterior part of body. *in,* intestine; *ov,* ovary; *te,* testis; *vi,* vitellarium or yolk gland.

lateral edges. Eyes are two, of regular size, placed close together and removed from the frontal margin. The specimens were immature when collected and were placed in a laboratory culture where they matured after several months. The length of the preserved mature worms is 6 mm, which would correspond to about 8–10 mm in life.

Anatomy.—Apart from the reproductive system, the general anatomy shows no peculiarities. The eyes are of normal size (diameter of the pigment cup 57 μm). The ovaries (Fig. 6) are hyperplastic, of enormous size, and consist of amply lobed and branched masses of darkly staining (cyanophilic) cells. Histologically, not all these cells are oocytes, but some, particularly in the peripheral portions, are comparable to those of parovaria. The yolk glands or vitellaria are very abundant and fully developed, occupying all spaces of the mesenchyme, beginning somewhat anterior to the ovaries and extending to the posterior end. The numerous testicular follicles are small, round, and located strictly ventrally, below the intestinal branches. The testicular zone on either side begins a short distance behind the ovary and reaches posteriorly to about the level of the mouth. In all three specimens examined, the follicles contain no ripe sperm cells, only immature spermatogonia.

The copulatory apparatus (Fig. 7) is rather small and not very clearly differentiated. The atrial cavity is undivided. The penis has a small weakly muscular bulb and a finger-shaped papilla. Its lumen consists of a bulbar cavity (seminal vesicle) lined with a tall glandular epithelium, and a narrow duct (ejaculatory duct) with cuboidal or flattened cellular lining, that runs through the center of the papilla and opens slightly dorsally to its tip. The vasa deferentia, which in other planarians appear widened, convoluted, and filled with sperm before entering the penis, forming the spermiductal for false seminal vesicles, are here empty and only slightly widened. They enter the penis bulb laterally and open separately into the seminal vesicle. The outlet of the rounded copulatory bursa takes an arch-shaped course, gradually widening in its posterior section, without forming a histologically dif-

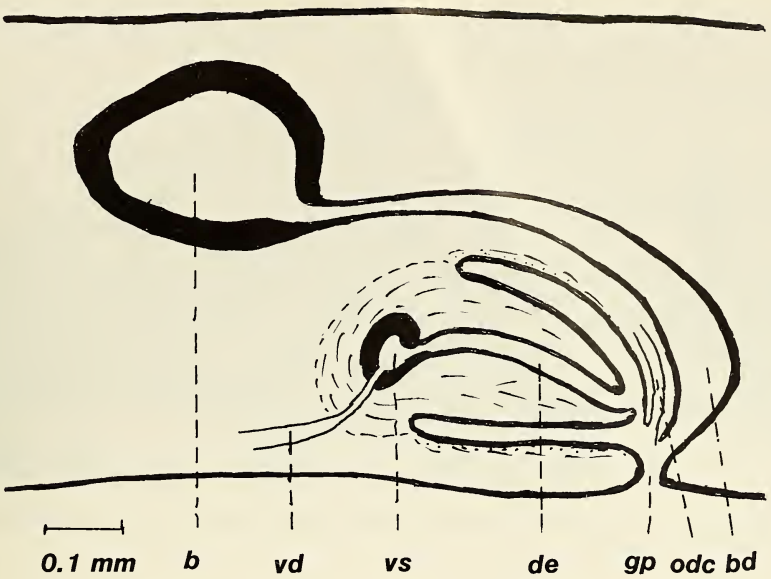

Fig. 7. *Phagocata spuria,* copulatory apparatus in sagittal section. *b,* copulatory bursa; *bd,* bursal duct; *de,* ejaculatory duct; *gp,* gonopore; *odc,* common oviduct; *vd,* vas deferens; *vs,* seminal vesicle.

ferent vagina. It opens into the atrial cavity near the gonopore.

Distribution and ecology.—The species is known only from Bennett's Mill Cave in McDowell County, North Carolina, located just outside the town of Marion. Cato O. Holler, Jr. collected 3 immature specimens on 12 Jun 1977 and sent them to me alive. They matured in the laboratory. No signs of reproduction, either by fission or by cocoons, were observed. Two specimens were preserved in Dec 1977 and the third in Sep 1978.

Taxonomic position.—While the general anatomical plan of the species places it clearly in the genus *Phagocata,* the specimens exhibit some characters rarely observed in planarians. The full development of the ovaries and yolk glands, together with the incomplete appearance of the testes, may seem to indicate that the female gonads mature at a time different from that of the male gonads. This would not, however, explain the remarkable hyperplasia of the ovaries which are generally rather small rounded organs adjoining the ventral nerve cords. This hyperplastic condition is occasionally observed in fissiparous races, such as has been reported for *Phagocata morgani* in Canada (Benazzi and Ball 1972) and for the European *Dugesia subtentaculata* (Draparnaud) and some related species (Benazzi 1968, 1974; Gremigni and Banchetti 1972; Benazzi and Deri 1980; de Vries 1986). Nonetheless, the anatomy of the penis and of the bursal duct separates *P. spuria* from other species of the genus.

Etymology.—The name *spuria* (Latin, spurious, false) alludes to the striking external similarity of the species to *P. morgani.*

Phagocata carolinensis Kenk
Fig. 8

This species was established and described by Kenk (1979) from One Bat Cave, Burke County, North Carolina. It is characterized by having a truncate anterior end with some lateral widening, but lacking prominent pointed auricles; it also has a pair of very small eyes. The most conspicuous anatomical feature is the presence of an exceptionally large posterior section of the

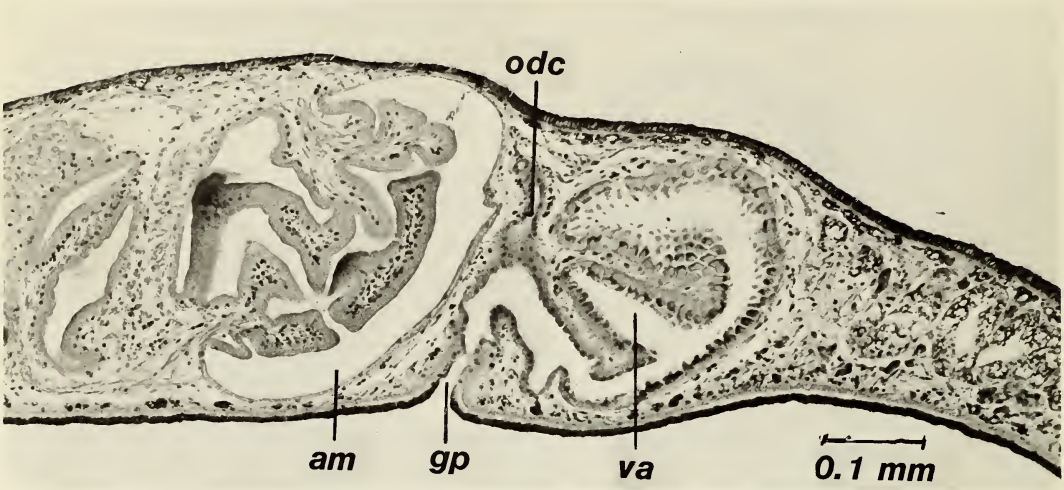

Fig. 8. *Phagocata carolinensis,* sagittal section through copulatory apparatus. *am,* male atrium; *gp,* gonopore; *odc,* common oviduct; *va,* vagina.

bursal duct, or vagina (Fig. 8, *va*), which may extend far posteriorly and is lined by a glandular epithelium differing from that of the anterior section of the duct. The vagina lacks any excessive muscular coating and may appear variously folded in the preserved specimens. The penis, which in its retracted state has a serpentine-like lumen shown in the original description of the species, may extend and assume an irregularly convoluted shape of the penis papilla (Fig. 8).

Additional material of the species was obtained from Wind Cave, McDowell County, North Carolina, located near Marion. It was collected by Cato O. Holler, Jr. on two visits to the cave; 4 specimens, some mature, taken from a small seep, 15 Apr 1984; and 5 specimens, all immature, collected beneath rocks lying on moist clay in an abandoned water course, 15 Feb 1985 (they were raised to maturity in the laboratory).

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